Mechanical properties of fish tail joints

Videler, J.J.

Published in:
Fortschritte der zoologie

Publication date:
1977

Sonderdruck aus «Fortschritte der Zoologie» Band 24, Heft 2/3 (1977)
Gustav Fischer Verlag Stuttgart · New York – Alle Rechte vorbehalten

Mechanical properties of fish tail joints

J. J. Videler

Zoological Laboratory, University of Groningen, The Netherlands

The scientific fields of physiology of movement and biomechanics incorporate a wide range of diverse subjects.

Before delving into the detailed problems an individual worker deals with in a topic like fish locomotion, it seems necessary to give a brief survey of the different aspects of this diversity.

Such a survey simultaneously gives me the opportunity to show where my own work fits into the whole range of fish locomotion studies. Thereafter, I will demonstrate something of this work by showing how some mechanical properties of joints between tail fin and caudal peduncle of the cichlid fish *Tilapia nilotica* (see plate 1) can be determined with the combined use of kinematical and morphological descriptions.

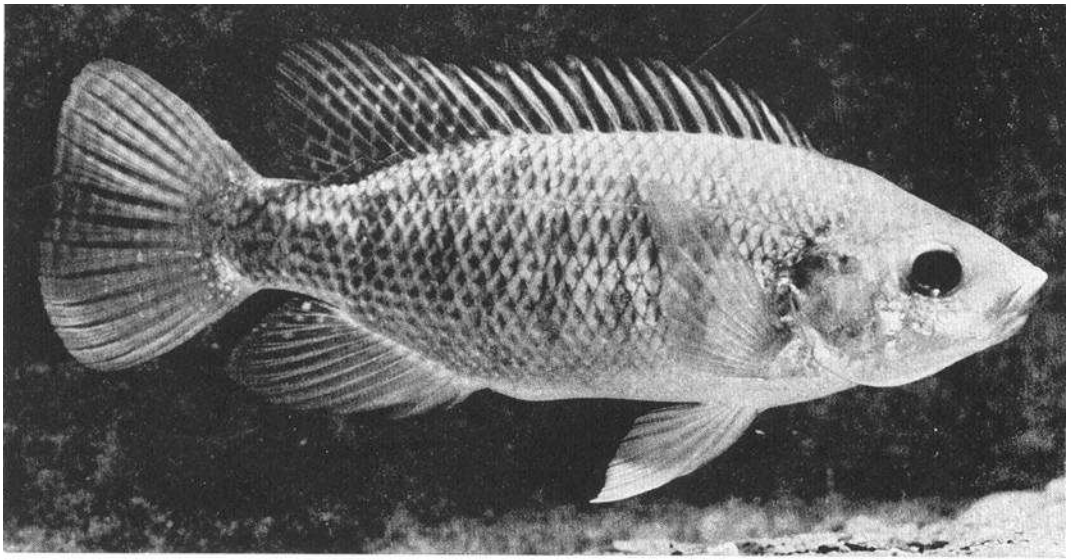

Plate 1: *Tilapia nilotica* (L.): a «typical fish».

1. General introduction

For convenience, I shall consider the diverse aspects of fish locomotion under functional and morphological approaches, although this subdivision is to a large extent an artifact.

2. Functional approach

Hydrostatic aspects: In theory it is possible to study a fish as if it were a submerged, motionless object. Such studies concentrate on the determination of the specific gravity; the center of gravity; and the center of hydrostatic pressure. The last two points are, mostly for reasons of convenience, said to coincide in fishes. There is not much evidence to justify this as the center of hydrostatic pressure has never, to my knowledge, been exactly determined in fish. Naval architects have demonstrated that one can determine the behaviour of a submerged object under several circumstances, using the knowledge of the exact position of both centers.

Authors who have paid attention to these aspects include Lowndes (1955), Aleef (1960), and Ohlmer (1964).

Kinematic aspects: Two different ways of describing movements of fishes can be thought of: A. a gross description of movements of the whole fish and B. a precise description of parts of a fish.

A. This kind of description of swimming modes requires series of frames of cine film on which the outlines of the fish are clearly visible, taken from the dorsal or ventral side together with some length reference.

Breder (1926) was very succesfull in the first way of describing movements, his classification of several types of swimming behaviour among fishes is still in use although it has been added to by several authors.

Fishes can be divided into two main groups on the basis of the structures used to propell themselves: into those using body and tail fin and those using median or pectoral fins.

This latter group is very diverse, including only a small number of species. The first group is of much more importance. Within this group three main ways of locomotion can be distinguished:

1. The anguilliform way: These fishes are elongate and laterally flattened. The whole body is thrown into a wave and there is at least one half to one wavelength on the body. The amplitude of the wave is usually large along the whole body.

2. The ostraciform way: The body of these fishes is short and rigid; the tail fin is the only part that oscillates.

3. The carangiform way: quoting Breder (1926): «The movements displayed by most typical fishes are intermediate between the two extremes just examined» (i.e. 1 and 2). The body oscillates with less then half a wave-length on the body, the amplitude of the wave is increasing backwards. These carangiform fishes are a very diverse and large group and I shall therefore, subdivide these for convenience according to Nursall's (1958) proposals.

He discriminated carangiforms, on the basis of morphological criteria, into: a. «Typical fishes», possessing a flexible tail fin with an Aspect Ratio ($span^2$/area) between 2 and 4, a broad muscular caudal peduncle and a flexible vertebral column with short vertebrae. The tail fin can be moved ray by ray and these fishes can show a wide range of swimming performances such as hovering, short range manoeuvering, quick starting or braking and sustained swimming.

b. Fishes with stiff tail fins with an Aspect Ratio between 5 and 6, a slender caudal peduncle without intrinsic muscles and a stiff vertebral column with long vertebrae. Swimming performance is more or less restricted to straight forward swimming and steering.

B. The second way of kinematic description, the precise recording of the movements of parts of a fish requires series of photographic pictures which show small details and allow measurements of movements of fins or even fin rays relative to each other. Brainbridge (1963) made films that were good enough to allow this kind of approach. I will show later on that this is the kind of kinematic description that provides sufficient details to piece movements and morphological structures together.

Hydrodynamic aspects: Studies of the interaction between water and the moving fish received a great deal of attention in the conferences on animal locomotion in Pasadena (1974) and Cambridge (1975). Webb (1974), in his very useful monograph on hydrodynamics and energetics of fish propulsion, summarises the results of the scientific efforts in this combined biological and physical field. From the numerous models describing the interaction between fish and water, Lighthill's (1969. 1970, 1971) reaction models are the most applicable. These models give estimates of thrust power of hypothetical fishes which are in good accordance with physiological estimates like maximum muscular power output.

For a biologist, these data are not completely satisfactory as a large discrepancy exists between the performance of these hydrodynamic models and the actual performance of swimming fish, even if they swim very steadily.

Energetic aspects: In this field the central theme is the relation between the total amount of energy spent by a swimming fish and the way the fish produces this energy. Oxygen consumption is normally used as a measure for energy spent during sustained swimming. During shorter swimming activities, anaerobic muscular effort makes this measure less useful.

In relation to this are the questions concerning efficiency of swimming in terms of efficiency of a propeller system, overall efficiency and optimum swimming speeds or modes (Webb, 1974).

3. Morphological approach

In talking about morphological structures it is obviously necessary to emphasize separately external features of unimpaired fishes and internal features, visible only after dissection.

The study of moving structures is closely related to and even overlaps the kinematic approach.

As for the unimpaired fishes, in the first place we have to study the movements of body and fins of a single species during different stages of its swimming performance. In the second place we must try to consider descriptions of external forms of numerous species in relation to kinematic classification.

Detailed anatomical descriptions of muscle-bone-connective tissue constructions have to show how movements can be carried out, how the movements are structurally limited and how the generated forces can be transmitted.

I stated before that this type of approach can only be successful if the cinematographic data are such as to show the movements involved in sufficiently fine detail.

In the next part I will show how mutual comparisons of descriptions of movements of caudal peduncle and fin of a «typical fish» with morphological descriptions of joints between fin rays and peduncle can help in elucidating the mechanical properties of the joints.

4. Methods

Movements of caudal peduncle and fin of *Tilapia nilotica* were studied in great detail by analysing, frame by frame, 16 mm cine film.

The freely moving animal was filmed at 25 frames per second from the lateral and ventral side simultaneously (for further details see Videler, 1975).

With the use of the resulting kinematic description a number of properties of the peduncle-fin connection could be postulated.

Morphological descriptions of the joints (shorn of details which I considered irrelevant with respect to mechanical functions) were made from series of transverse and frontal sections of the entire tail region. The resulting model had to fulfil the requirements indicated from the kinematic description.

5. Results

5.1. Kinematic description

Tilapia nilotica is a highly mobile type of fish, able to perform complicated swimming manoeuvers at close range. In order to simplify matters a considerable restriction was made. This analysis contains data concerning only the movement of fin rays with regard to the caudal peduncle during locomotion in straight forward direction.

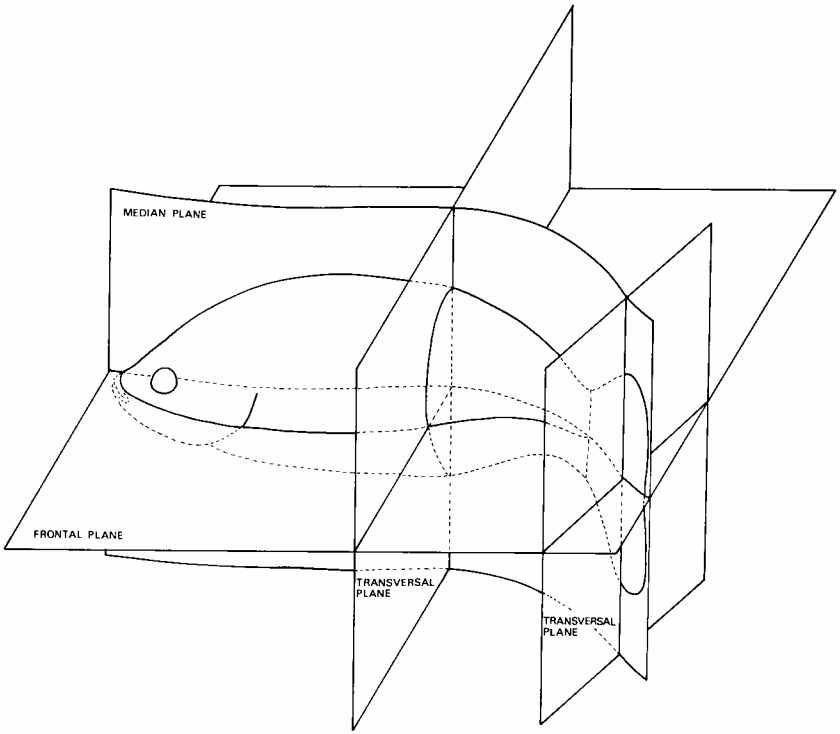

Fig. 1: Planes of reference, used in the description of structures and movements of *Tilapia nilotica*. From Videler, 1975.

I will only consider movements in the frontal planes through the middle and through the edge of the fin and movements in the median plane (see figure 1).

Figure 2 shows how several tail strokes have been represented. The central lines of the ventral views of the body and the mid-line of the fin are drawn to represent the movements in a frontal plane through the middle of the fin. (The mid-line of the fin could be determined exactly on the frames of cine film by means of a black thread attached along the fin.)

Strokes A, B, C and D represent 4 different tail strokes. Stroke A is the most vigorous type, amplitudes of the end of the peduncle and of the fin edge being large. Stroke D exemplifies the other extreme. Strokes B and C are intermediate types, in which the amplitudes of the peduncle are equal, but the amplitude of the fin edge of stroke B is about twice as big as the one of stroke C. There are two conceivable

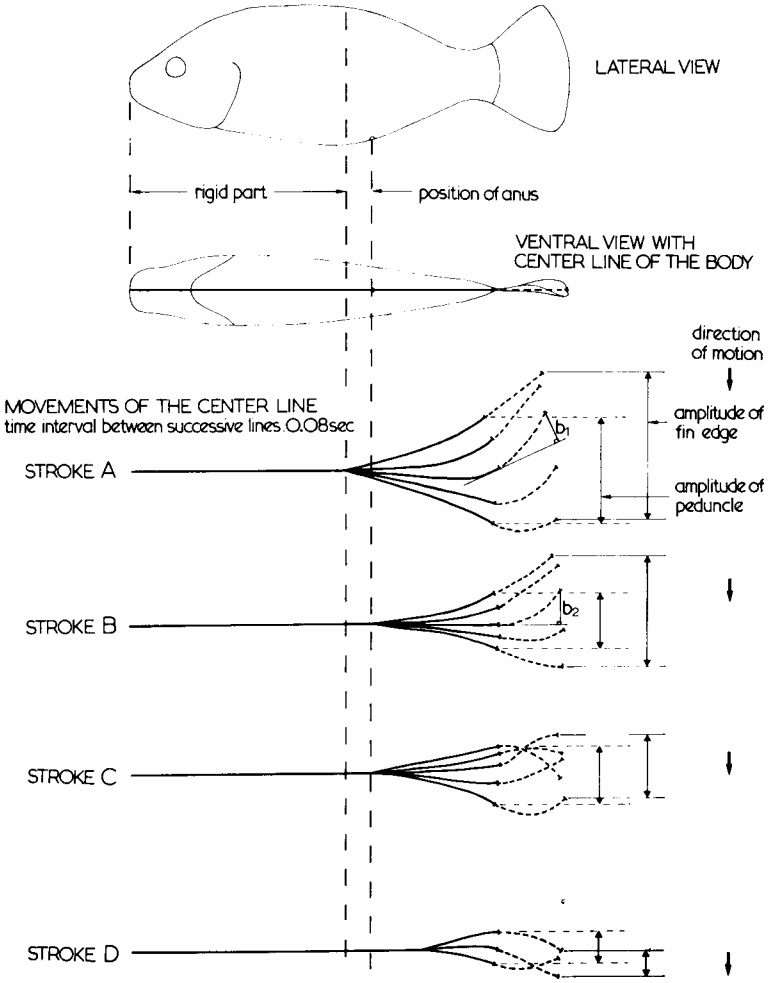

Fig. 2: Different tail strokes of *Tilapia nilotica* represented by central lines of the body and mid-line of the fin as seen from the ventral side. From Videler, 1975.

ways in which this phenomenon could occur: 1. The bending properties of the fin rays are not constant. 2. The connection between peduncle and fin rays is not a rigid one.

We can find proof for the changing bending properties of fin rays in figure 2 if we compare the amount of bending (expressed as the length of the perpendicular from the fin edge onto the tangent to the proximal part of the fin (b)) in the midstroke situations in stroke A and B. As there is a constant time interval between the successive lines, strokes A and B take an equal time. Consequently the lateral speed of the fin during stroke A exceeds the speed of B. The amount of bending (b_1) in the midstroke situation of A, however, is considerably smaller than b_2 of the slower stroke B. This means that the bending property must have changed.

In figure 2 it is hard to see whether the angle between the central line of the body and the tangent to the proximal part of the fin changes. Therefore it is necessary to analyse the peduncle-fin connection more closely. Figure 3 shows how the angle be-

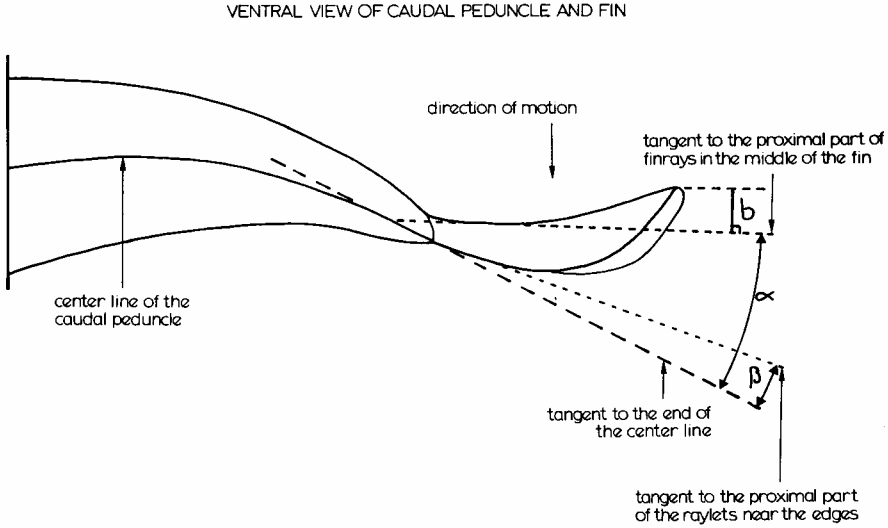

Fig. 3: Method of measurement from the ventral view of the caudal peduncle and fin of *Tilapia nilotica*. From Videler, 1975.

tween the tangent to the proximal part of the fin rays near the mid-line of the fin and the tangent to the end of the central line (angle α) can be measured from a magnified frame of cine film. The same figure shows also the angle β between the tangent to the central line and the tangent to the proximal part of the raylets in a frontal plane through the ventral edge of the fin. The angles α and β are called positive when the fin rays lead in the direction of motion and negative when the fin rays lag behind. At the turning point of a fin stroke the fin rays have to execute a rotation of twice the value of these angles, assuming that the angles are equal during fore and backstroke. A change of angle always occurs near the turning points.

Values of these angles, measured near the midstroke position, are:
Mean value of angle α: −10°, extremes: + 7° and −35°.
Mean value of angle β: − 5°, extremes: + 3° and −19°.

Figure 4 shows how a reconstruction of the caudal view of the highest part of the fin can be made using data from the lateral and ventral views. This caudal view provides information about the curvature of the fin and about the amount of spreading of the fin. This spreading is caused by abduction of the fin rays. The biggest change in the surface area of the caudal fin of *Tilapia nilotica*, measured during series of fin strokes, was an increase in the area of 53 %. (For further details see Videler, 1975).

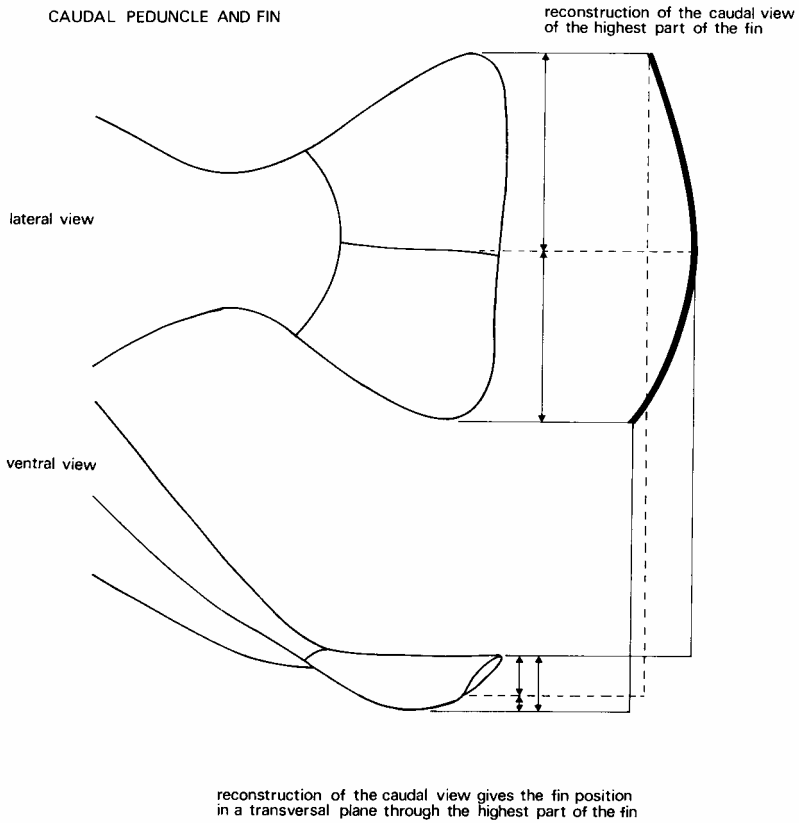

Fig. 4: Method of reconstruction of the caudal view of the highest part of the fin, using data from the lateral and ventral views. From Videler, 1975.

X-ray photographs of tail fins of anaesthetised fishes show that the maximum abduction/adduction angle of fin rays near the mid-line of the fin is about 5°.

The kinematic approach briefly described above leads to the following predictions, regarding the properties of the fin ray – peduncle connection:

1. Peduncle and fin can act as one plane during the effective part of a tailstroke. This means that there must be a very firm connection during this phase of the movement.

2. The caudal fin acts as the main propellor, thus forces in cranial direction have to be transmitted via the fin ray joint to the vertebral column. This has to be done with as little loss, due to elasticity, as possible.

3. An active change in bending properties of fin rays during tail strokes must be carried out by the structures involved.
4. A variety of angles between fin rays and peduncle in the frontal planes must be possible. These angles are fixed during the effective part of the stroke.
5. The connection has to allow abduction and adduction movements.

5.2. Morphological description

Structure of fin rays and raylets.

The tail fin of *Tilapia nilotica* usually has 16 branched finrays, 8 in the dorsal and 8 in the ventral half. In addition, there are 4 and 5 unbranched raylets lying dorsally and also ventrally to these fin rays. The fin rays and raylets are, basically, built out of numerous small pieces of bone interconnected by collagenous fibres and covered with skin. They consist of two halves, one on the right and one on the left side of the fish, which are exact mirror images of each other. Figure 5 gives some important details of this construction. The lateral view of the fin ray shows how the branching increases to the rear. Dichotomy does not occur equidistantly in different branches, but in the right and left half of the fin ray the division of the bony pieces is exactly the same.

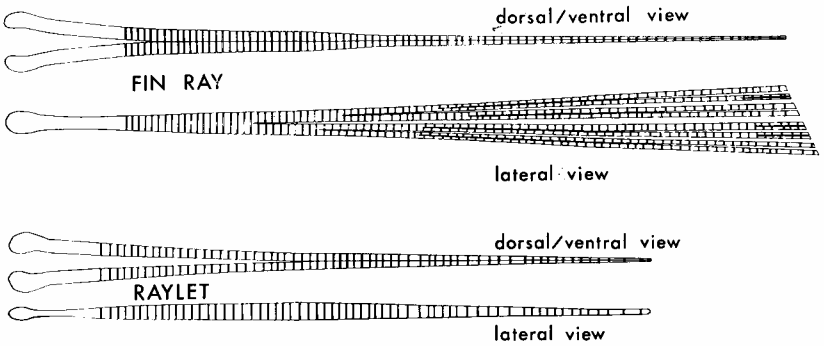

Fig. 5: Reconstruction of a fin ray and a raylet of the tail fin of *Tilapia nilotica*.

The dorsal and ventral views show that the bony pieces of the right and left halves are equally large and lie exactly opposite to one another. The bony segments of the raylets do not branch. The proximal part of each half of a raylet or ray consists of a somewhat swollen head with a slightly constricted neck behind it. The right and left head are slightly bent towards each other as is seen in the frontal plane.

The joints between fin and caudal peduncle.

The vertebral column of bony fishes usually ends as a triangular bony plate. This occurs in such a way, that one of the sides of the triangle is the distal end of the bony axis of the fish. This bony plate is called the ural fan and it ends between the left and right heads of the fin rays and the raylets. Figure 6a shows a schematic frontal section of this construction. The distal part of the ural fan is covered on the right and left side with a cushion of connective tissue. The end is rounded and made out of cartilage.

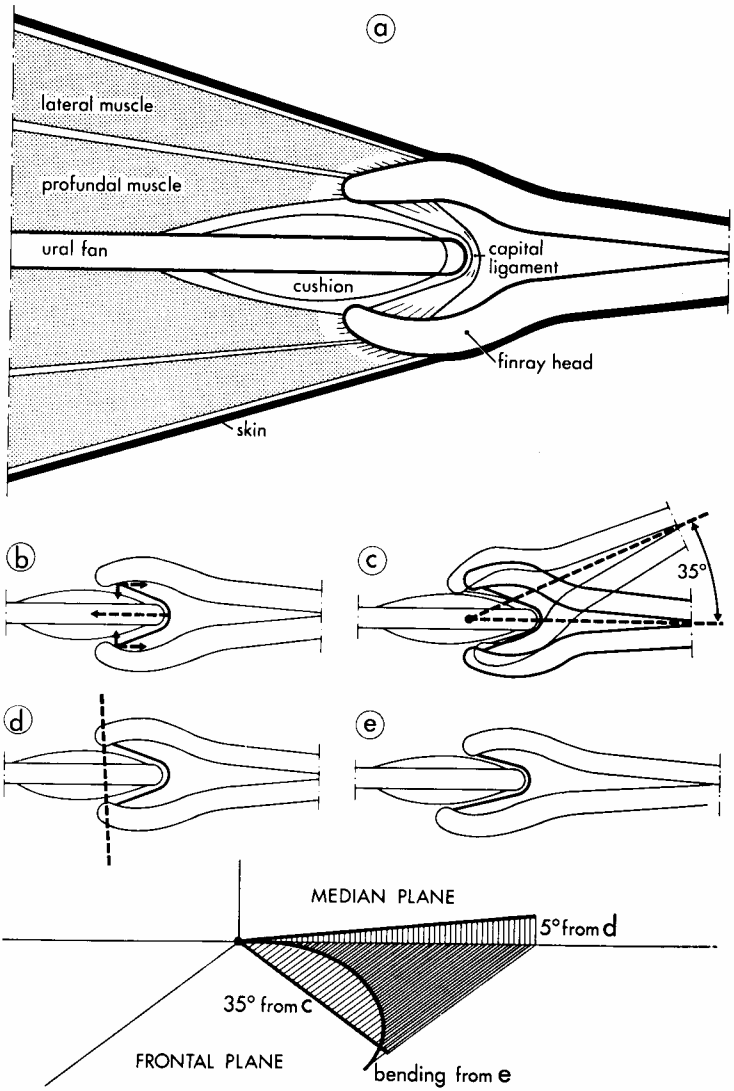

Fig. 6: Structure and mechanical properties of a tail fin joint of *Tilapia nilotica*.

A tough collagenous ligament, the capital ligament, is attached to the medial side of each fin ray head and runs caudally around the end of the ural fan. The lateral musculature, profundal muscles as well as the skin are firmly attached to the heads of the fin rays. The situation near the ventral and dorsal edge is somewhat different. Here the heads of the raylets are buried in the connective tissue and the capital ligament is very short. There are direct collagenous connections between the heads of the raylets and the ural fan.

6. Discussion

I now want to relate the 5 predictions obtained from the kinematic approach with the structures described in the morphological approach. During the effective part of a tail stroke the tail fin propells the fish and this means that there is a force in a forward direction along the fin rays. Figure 6b shows how the joint can deal with such a force. The capital ligament will be tightened around the end of the ural fan and the slightly bent fin ray heads undergo a force in the direction of the ural fan. The result, in such a situation is, that the ural fan is pinched between the fin ray heads, and the stiffness of the connection is increased by the cushion of connective tissue. An advantage of this system is that the propulsive force itself determines the stiffness of the connection. Thus, if the fish uses his tail as a manoeuvering device without much propulsion, the connection can be quite flexible.

Propulsive forces are transmitted along the fin rays and raylets towards the incompressable vertebral column. The capital ligament is the only link in the chain between ray and vertebral column not made out of bone. The toughness of the bundle of collagenous fibres shows that there will be little or no loss due to elasticity here. Near the dorsal and ventral edges this connection is even better because there is an additional collagenous connection between the heads of the raylets and the ural fan. Even forces in caudal direction (braking forces) could pass these joints without losses.

Figure 6c shows the proximal part of a fin ray after maximum rotation in a frontal plane. The maximum rotation the construction allows is about 35° and this is in per-

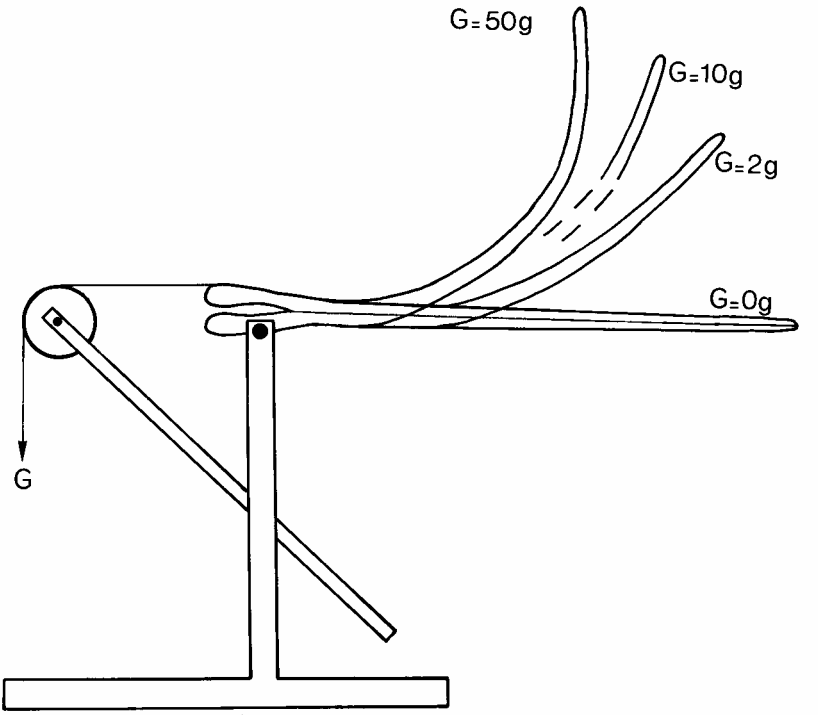

Fig. 7: Bending of a fin ray by forces inserting on the fin ray heads.

fect accordance with the maximum angle found during the kinematic analysis. The construction of the cushion and the length of the capital ligament make tightening of the connection possible, even if the angle between fin ray and ural fan is extreme.

Figure 6d shows the axis of the adduction/abduction movements of the ray. The axis runs through the fin ray heads near the insertion of the capital ligament. The rigidity of the system due to pushing and pinching forces does not have much influence on the movability of the joint in the median plane, because the capital ligament is not involved in this kind of movement.

A simple experiment gives an indication of how a fish can control the bending properties of its fin rays with no other muscles than the ones inserting on the fin ray heads. Figure 7 shows a fin ray attached with one head in a clamp, a weight G pulls the other head in a direction along the fin ray. Different weights produce different bending of the distal end of the ray by shifting the proximal part of one fin ray half with respect to the other.

In the fish this mechanical system is used in a slightly different way. During an effective tail stroke the water will try to bend the fin in a lateral direction, opposite to the direction of motion. This bending action of the water will cause the same shifting effect between the proximal parts of the fin ray halves as in the experiment (see figure 6e). The profundal muscles can easily counteract this movement of the fin ray halves and in doing this change the bending properties of the fin rays. McCutchen (1970) gives more details about the mechanics of this bending phenomenon, but he overlooks the active role the fish has in it. In my opinion an important factor in the locomotion of «Typical fishes» is the fact that the fish can actively increase the stiffness of the fin. The effect of a stroke is greatly determined by the stiffness of the tail fin because this determines to a great part the angle of attack of the fin.

Acknowledgements

I want to thank my friends and colleagues G. Thomas and P. J. Geerlink for their help and interest. Thanks are due to the administrative and technical staff of the biological center for the assistance in preparing the manuscript in the middle of a hot summer.

References

Aleef, Y. G.: Function and gross morphology in fish. Jerusalem, Israel program for scientific translations (1970).

Bainbrigde, R.: Caudal fin and body movement in the propulsion of some fish. – J. Exp. Biol. *40*, 23–56 (1963).

Breder, C. M.: The locomotion of fishes. – Zoologica *4*, 159–297 (1926).

Lighthill, M. J.: Hydromechanics of aquatic animal propulsion. – Ann. Rev. Fluid Mech. *1*, 413–446 (1969).

– Aquatic animal propulsion of high hydromechanical efficiency. – J. Fluid Med. *44*, 265–301 (1970).

– Large-amplitude elongated-body theory of fish locomotion. – Proc. R, Soc. Lond. Ser. B Biol. Sci. *179*, 125–138 (1971).

Lowndes, A. G.: Density of fishes. – A. M. N. H. Ser. 12, *8*, 241–256 (1955).
McCutchen, C. W.: The trout tail fin: a self-cambering hydrofoil. J. Biomechanics *3*, 271–281 (1970).
Nursall, J. R.: The caudal fin as a hydrofoil. – Evolution *12*, 116–120 (1958).
Ohlmer, W.: Untersuchungen über die Beziehungen zwischen Körperform und Bewegungsmedium bei Fischen aus stehenden Binnengewässern. Zool. Jb. Anat. Bd. *81*, 151–240 (1964).
Videler, J. J.: On the interrelationships between morphology and movement in the tail of the the cichlid fish *Tilapia nilotica* (L.). Neth. J. Zool. *25* (2), 143–194 (1975).
Webb, P. W.: Hydrodynamics and energetics of fish propulsion. – Bull. Fish. Res. Board Can. *190*, 159 p. (1974).